

FINAL REPORT

STUDIES ON WESTERN SPRUCE BUDWORM
POPULATION DYNAMICS

Co-Investigators: Robert W. Campbell and Torolf R. Torgersen

Organization: Pacific Northwest Forest and Range Experiment Station

Forestry Sciences Laboratory

Corvallis, Oregon 97331

and

Range and Wildlife Habitat Laboratory

La Grande, Oregon 97850

Cooperators: Roy C. Beckwith, Nilima Srivastava, Kevin Hosman,

Daniel B. Twardus, Larry Stipe, Edward O. Garton.

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SUMMARY

Fellin and others (1983) summarized the history of the western spruce budworm in the northern Rocky Mountains as follows:

Two infestations were reported near Priest Lake in northern Idaho [in 1922]. Over the next 30 years, only scattered and insignificant infestations were reported.... The first significant outbreak... began about 1948 and has persisted until now [1983].

In short, budworm populations are usually either at densities where they are barely discernible by standard sampling techniques, or at densities so high that defoliation is obvious. Populations of intermediate density are in transition--either increasing to outbreak, or decreasing to sparse. The significance of this pattern is that it focuses attention on the two major population modes (outbreak and sparse) and two transient phases (release and decline) where we must have information for evaluating and understanding numerical changes. Processes that appear to dominate each mode or phase of this life system (sparse, release, outbreak, and decline) are summarized below.

Sparse Mode

Poor survival is characteristic from fourth instar to pupae remaining after predation (residual pupae) among sparse, stable populations. At least in the northwestern United States, this low survival is established largely through predation by birds and ants. Unless unusually high survival or inward migration occurs during other stages, this predation appears adequate to maintain populations at sparse densities indefinitely.

Release Phase

Either (or both) of two major events are sufficient to enable a sparse population to increase to an outbreak. One is high survival during dispersal (fall and spring) of small larvae; the other is redistribution of egg masses by gravid females.

High survival during larval dispersal is associated with abundant host foliage, multistoried stands, and a particularly favorable conjunction between spring budburst and emergence of the larvae from hibernation. Relatively little is known about the redistribution of eggs by adult females, but the adult insects appear particularly likely to lay their eggs in the tops of older trees (Campbell and others 1983d). Thus, flying adults may be particularly likely to land in either old growth or stands with a prominent silhouette.

Outbreak Mode

Once an outbreak starts, declining survival among young larvae (probably primarily caused by competition for feeding sites during spring dispersal) appears to be important in maintaining the outbreak from one year to the next. During outbreaks, this survival rate appears to decrease as density increases. This phenomenon undoubtedly reduces the chance that later instars will exhaust the foliage and starve.

Decline Phase

Outbreaks may decline through any combination of processes that can operate against dispersing small larvae, larger larvae, residual pupae, or adult moths.

Exceptionally low survival of the small larvae could be caused by differences in timing between larval emergence from hibernation and budburst, late frosts that destroy both the new foliage and the budworm, or foliage depletion through previous defoliations. Survival of the larger larvae is also at risk where most of the foliage has already been destroyed.

Parasitism among the residual pupae, which tends to be highest in places where mortality during earlier stages had already been high, may accelerate the collapse of an outbreak. Adult moths are also likely to disperse to other sites with little suitable foliage for laying eggs.

INTRODUCTION

Historically, forest managers have been most interested in forest pests after they reach high densities and threaten forest productivity or value (Mason 1979). Obtaining knowledge on how or why potentially damaging pest populations behave at sparse densities has been secondary. Now, however, primary interest in the western budworm has shifted toward preventing possible future outbreaks through judicious management. To design appropriate preventive practices, managers need to know a great deal about both the processes that maintain populations at sparse densities, and the processes that upset this stability and lead to outbreaks.

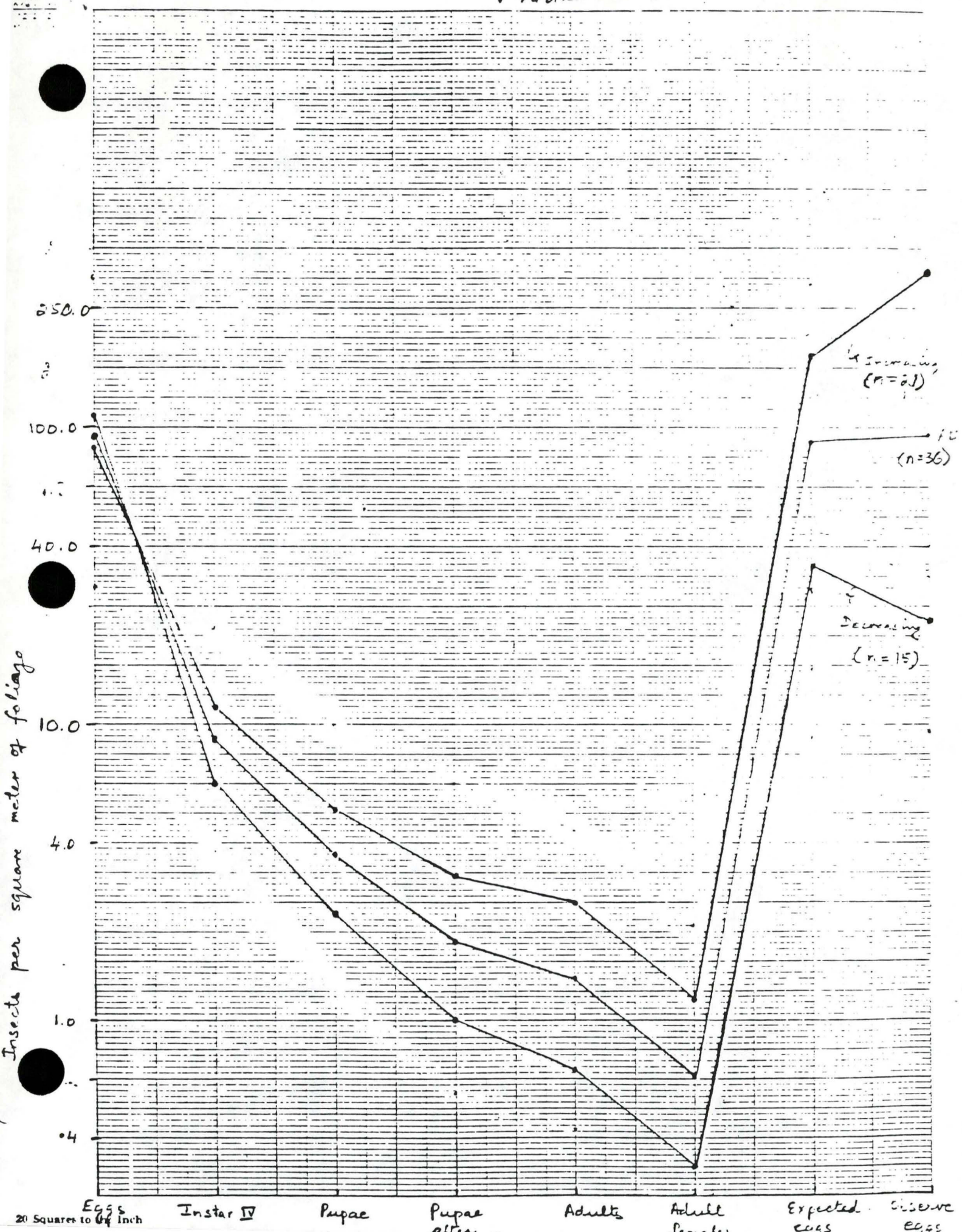
Life tables represent an important tool for studies on population dynamics. One table can summarize much biologically rational information about a sequence of densities, mortality-causing factors, and fecundity in one place and budworm generation. Although life tables for forest insects go back at least as far as Tothill's work (1922), their usefulness was not recognized by many investigators until the classic paper by Morris and Miller (1954) on the development of life tables for the eastern budworm. Morris (1955) also described a pattern for developing sampling methods for the eastern budworm that has been widely adapted by other workers. With these methods, investigators can estimate densities per unit of foliage area with specified confidence.

McKnight (1971) adapted Morris's methods to develop budworm life tables in Colorado. Carolin and Coulter (1972) also adapted these methods to develop sampling procedures for budworm in eastern Oregon. More recently, Campbell and others (1983a) used or adapted these methods to develop life tables for budworm in the Pacific Northwest.

Between 1978 and 1982, 36 life tables were accumulated on populations of budworm in Washington (10), Oregon (8), Idaho (10), and Montana (8). Twenty-one of these populations increased in egg density across a generation and 15 decreased. Successive average densities are shown in figure 1 for both the populations that increased and those that decreased. For almost every successive age interval, average survival was higher among populations that increased. Processes operating during each of these age intervals are discussed in following sections.

Figure 1.--Successive average densities among western budworm populations. Data from populations studied in the Pacific Northwest (1978-82).

FIGURE #1



METHODS AND PROCEDURES

Methods used to accumulate the data summarized in this report are described in several papers including the following: Campbell and others (1983a), Campbell and others (1981), Srivastava and others (1982 unpubl.). In each section of the report, reference is made to the appropriate paper(s) for methods and procedures.

RESULTS AND THEIR SIGNIFICANCE

LIKELIHOOD AND PERSISTENCE OF OUTBREAKS

East of the Cascade Range, detectable populations of the western budworm appear to persist indefinitely in stands that contain a substantial proportion of suitable hosts. Populations in these stands have exhibited one of three numerical patterns. First, the insect has been a chronic problem in many stands, particularly in Montana and Idaho. In one extreme outbreak, visible defoliation was recorded for 29 successive years. Thirteen of 91 documented outbreaks (14 percent) persisted without a break for at least 9 years; 32 of 91 (35 percent) persisted for at least 4 years (Johnson and Denton 1975). Second, outbreaks may only last for 1 or 2 years. Even in the northern Rocky Mountain area reported by Johnson and Denton (1975), 44 of 91 outbreaks (48 percent) persisted for only 1 or 2 years.

Persistence at sparse densities is the third numerical pattern exhibited by the budworm. Unfortunately, only a few records document this sparse pattern. Unlike outbreaks, which are obvious, sparse populations are only detectable by sampling.

Outbreaks Versus Weather

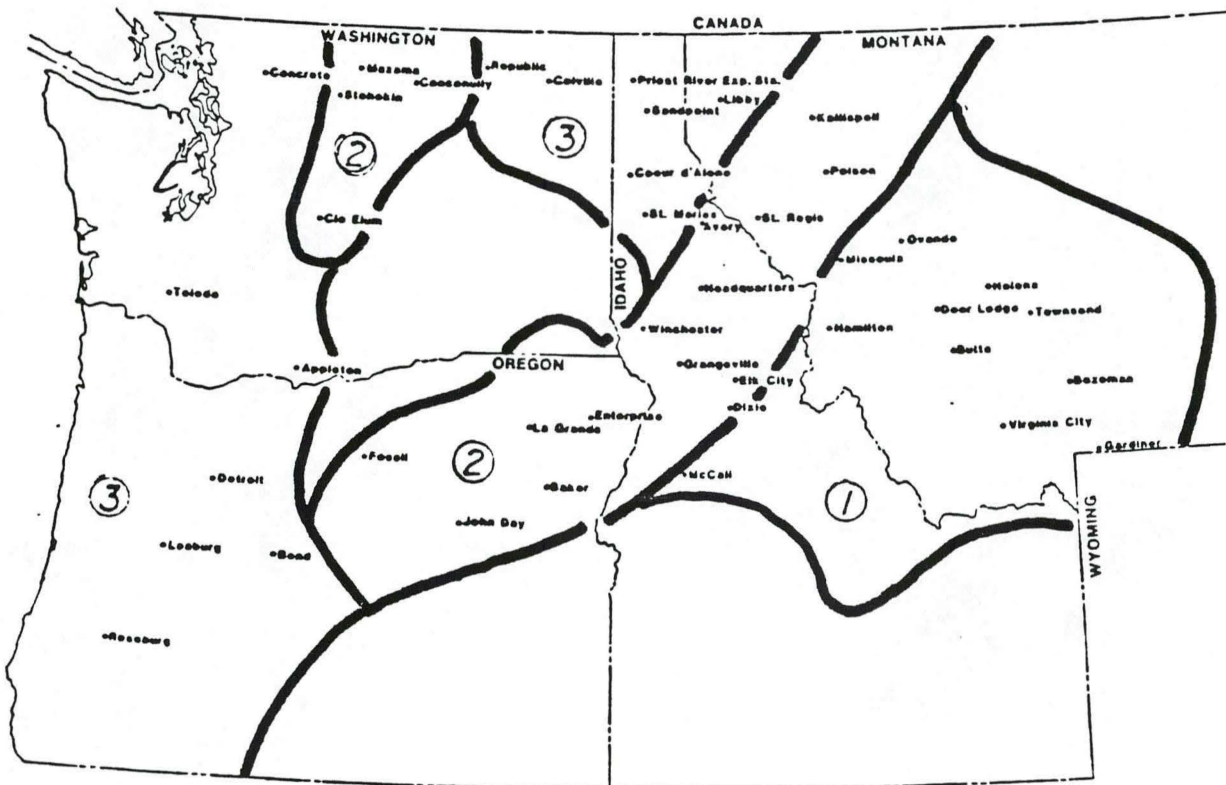
Several investigators have found correlations between warm, dry periods and subsequent outbreaks in both the eastern and western budworms. Hard and others (1980) examined records from northwest Montana and northern Idaho. They found that defoliation varied with weather during May, June, and July of the previous year--directly with mean maximum temperature and inversely with the frequency of days with measurable precipitation.

Similarly, Twardus (1980) found that warm, dry periods often preceded outbreaks in north-central Washington. Blais (1957a, 1968) associated eastern budworm infestations with dry summers and suitable densities of host species.

Recently, Kemp (1983 unpubl.) examined several climatic features in the Pacific Northwest (Washington, Oregon, north-central Idaho, and western Montana) to determine their association with budworm outbreaks. Kemp found three broad classes of outbreak frequency in the forested areas of the four states (fig. 2). He concluded that outbreaks were associated with drier climates, and that outbreaks occur most often in a fairly limited range of mean temperatures in January and July. Generally, outbreaks occurred where annual precipitation was between 9 and 36 inches (23 and 91 cm). Outbreaks were also associated with January mean maximum temperatures between 26 and 38° F (-3 and 3° C); with January mean minimums between 3 to 23° F (-16 to -5° C); with July mean maximum temperatures between 75 and 90° F (24 and 32° C); and with July mean

Figure 2.--Frequency of budworm outbreaks in forested areas of Idaho, Montana, Oregon, and Washington (high outbreak frequency = 1, medium outbreak frequency = 2, low outbreak frequency = 3) (after Kemp 1983 unpubl.).

FIGURE 2



minimum temperatures between 40 to 53° F (4 to 12° C). Links between climatic trends and defoliation frequency remain somewhat obscure. Kemp speculated that this linkage may be through increased host-plant stress and increased insect survival.

Kemp did not analyze weather trends that might be associated with the end of an outbreak. Once a population is released, adverse physical factors--such as cold, wet summers--may not bring either the eastern or western budworm under control (Greenbank 1956, Thomson and others 1983 unpubl.).

EARLY SURVIVAL

Among the Northwest populations studied between 1978 and 1982, survival from eggs to fourth instars (early survival) ranged across about 15-fold, from about 30 percent down to about 2 percent. Carolin and Coulter (unpubl.) estimated that survival from egg hatch to fourth instar was 43 percent in one plot, 7 percent in a second, and 6 percent in a third. Carolin later judged the lower survival (6 to 7 percent) to be more typical (Carolin, pers. commun.). In contrast, McKnight (1971) described average early survival of 64.9 percent for the populations he studied in Colorado between 1964 and 1966. The survival rates calculated by McKnight, however, use uncorrected estimates of density on midcrown branch tips. When these data were corrected to represent the whole plot, average early survival in these populations was estimated to be 18.8 percent (Srivastava and others 1982 unpubl.).

Density Versus Early Survival

Egg densities ranged from about 3 to 1,000 eggs per square meter among the Northwest populations studied between 1978 and 1982. Across this range, almost no correlation was found between egg density and early survival ($r^2 = 0.08$).

Some populations studied recently in northern New Mexico (Stein and McDonnell 1982 unpubl.) were commonly much denser than any of the Northwest populations. Among these New Mexico populations, early survival declined from 5 percent in places and years where egg density was lowest to only about 0.1 percent where it was highest (fig. 3). Thus, early survival became a function of density above a threshold somewhere between 500 and 1,000 eggs per square meter. Some likely consequences of this relation are discussed in subsequent sections of this report.

Components of Early Survival

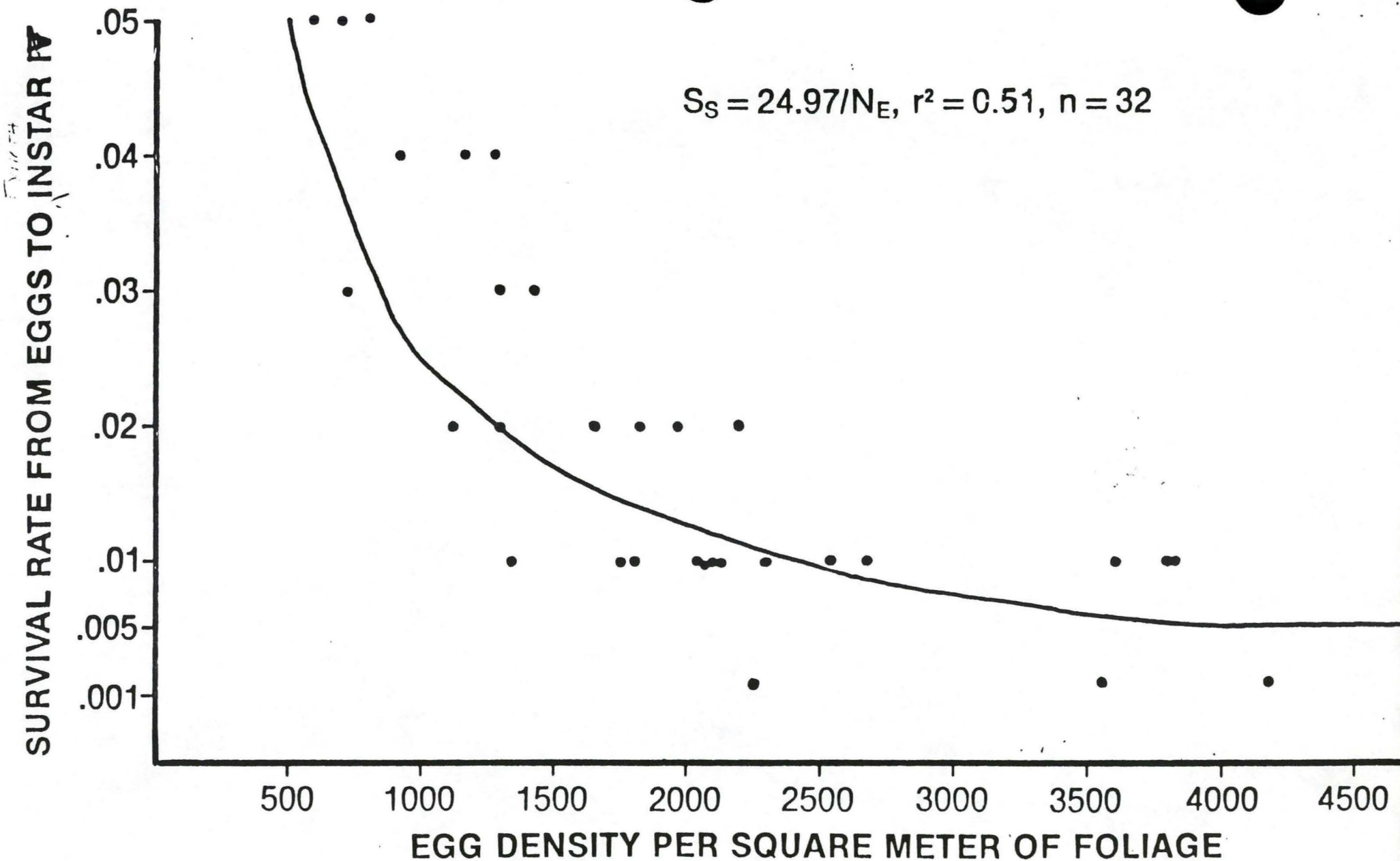
Egg Survival

The incubation period is brief; hatching occurs about 10 days after the eggs are laid (Carolin and Coulter 1972). During this interval, the eggs are at hazard from parasites and predators and may fail to hatch from other causes.

Average hatch was 93 percent among populations studied recently in the Pacific Northwest. Parasitism was generally extremely low, averaging only 1.2 percent (Torgersen and others 1983). Average mortality from all other factors was 5.4 percent. Carolin (unpubl.) also found high survival among eggs.

Figure 3.--Egg density versus subsequent survival from eggs to fourth instar (early survival). Data from northern New Mexico (1978-81). Several assumptions had to be made to estimate egg densities and survival rates from the original data (adapted from Stein and McDonnell 1982 unpubl.).

SURVIVAL FROM EGGS TO INSTAR IV



Fall Dispersal

Only a few estimates of fall dispersal have been made for western populations. After intensive study in two sites in north-central Washington, Eldridge and Egan (1983 unpubl.) found that survival during this interval was 39 percent in one site and 77 percent in the other.

Dispersal from the egg mass is initiated as soon as the larvae hatch. Larvae on silk threads can be carried long distances by the wind (Henson 1950), but the larvae generally hibernate within a few hours of hatch (Morris and others 1958a). During this brief interval, the larvae are at risk from spiders and other predators. Most of their mortality, however, can be attributed to dispersal.

Dispersal losses increase as the density of host trees decreases, and as the host stand becomes more isolated (Morris and Mott 1963). Miller (1958) characterized survival during this interval as more variable than survival among either eggs or larvae in hibernacula.

Hibernation Survival

Survival across this interval is both high and relatively invariant. From studies on two populations in north-central Washington, Eldridge and Egan (1983 unpubl.) found that survival was 79 and 87 percent. Remarkably similar survival (78 to 91 percent) was reported by Miller (1958) in New Brunswick. Terrell (1959) also reported generally high and invariant survival for hibernating larvae in the northern Rocky Mountains.

Spring Dispersal

Most of the variability in survival during the spring appears to be a consequence of variable losses from dispersal. Multiple dispersal episodes may be common, at least under some stand conditions. For example, Beckwith and Burnell (1982) found that dispersal of third and fourth instars represented about 38 percent of the larvae caught in dispersal traps in a mixed stand of Douglas-fir and western larch.

Spring dispersal begins as soon as the second instars emerge from hibernation. In northern New Brunswick, birds do not feed on young larvae of the eastern budworm (Cheshire 1959), but the larvae are again subject to predation by spiders and insects, as they are during fall dispersal (Mott 1963).

Whether dispersing larvae live or die is largely a question of whether they find a hospitable site (Mott 1963). As in the fall, spring survival is directly related to the density of host trees and inversely to the degree of isolation of the host stand (Morris and Mott 1963).

Recommendations for control through silviculture are based largely on relations between the amount and placement of host foliage and the dispersal requirements of the larvae (Carlson and others 1983, Schmidt and others 1983, Wulf 1982 unpubl.).

In addition to problems with movement between hibernation site and suitable foliage, insects emerging from hibernation must also deal with possible asynchrony between their emergence and the availability of suitable food. In populations of the eastern budworm, for example, Blais (1957b) showed that low survival on black spruce, Picea mariana (Mill.) B.S.P., results from delayed budburst.

Losses during spring dispersal may reflect the probability that the larvae will find suitable food before their energy reserves are depleted. For example, an extended period of warm fall weather may critically deplete these reserves among the larvae that will have to find suitable feeding sites after they emerge from hibernation (McMorran 1973).

Recently, Thomson and others (1983 unpubl.) analyzed relations between budworm outbreaks and long-term weather in British Columbia. They concluded that outbreaks were triggered by warm, dry summers in conjunction with optimal timing between larval emergence and the flush of Douglas-fir buds. All five outbreaks recorded among the records analyzed by Thomson and his colleagues "resulted only when a warm dry summer followed an optimal [spring] phenological relationship."

As reported earlier, early survival was inversely related to density, at least among dense populations in northern New Mexico. In all probability, this inverse relation reflects some sort of intraspecific competition among the larvae. Such competition seems most likely either

in the fall--for places to hibernate--or during the following spring--for suitable needles and buds. If this inverse relation between density and early survival proves to be generally true, it will likely also prove to constitute a potent process in the population dynamics of the pest. Specifically, such a process would thin overly dense egg populations to densities that would minimize the chance of exhausting the host foliage and subsequent mass starvation. Such a process would tend to insure that ongoing outbreaks will persist.

LATE SURVIVAL

Density Versus Late Survival

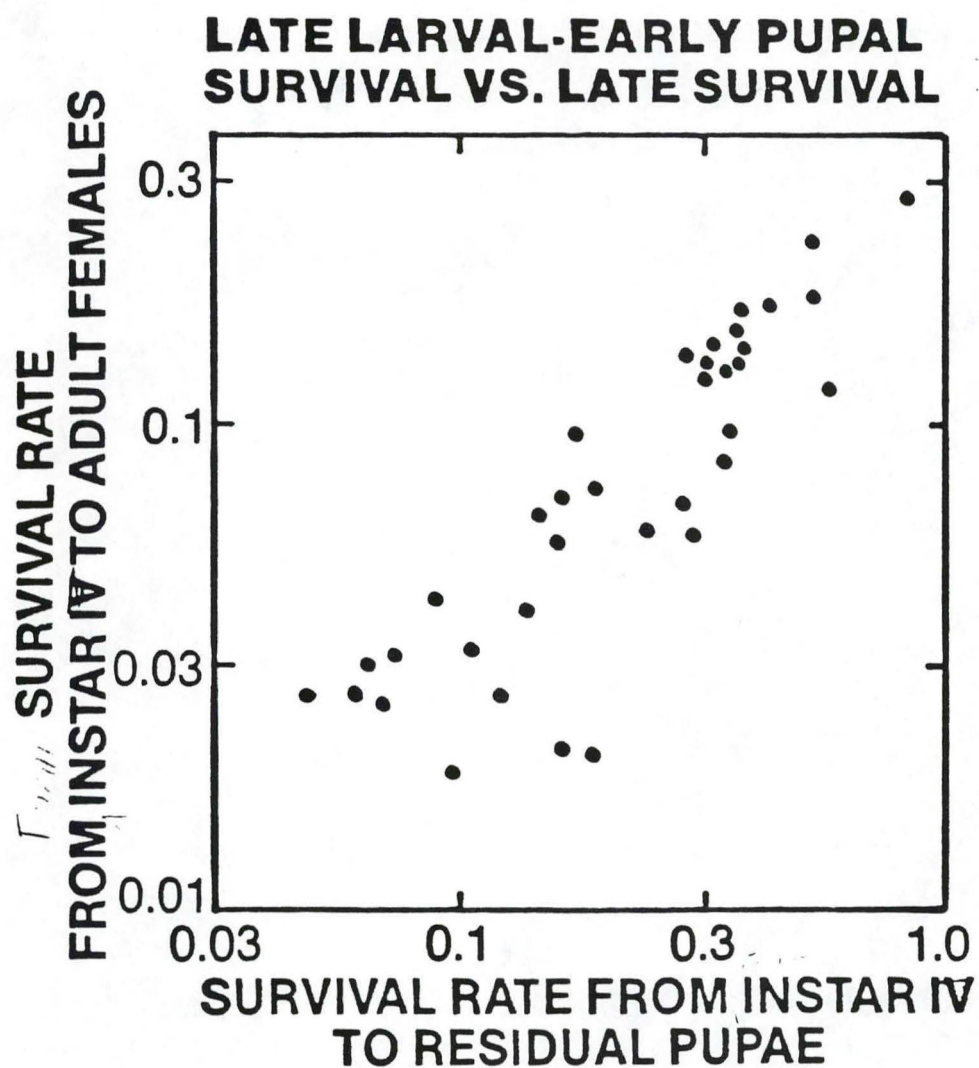
Fourth-instar densities ranged from about 0.3 to 80 larvae per square meter among the populations studied recently in the Northwest. Among these populations, survival from fourth instar to adult females (late survival) ranged across about 15-fold, and like early survival, ranged from about 30 down to 2 percent. Late survival was uniformly low among populations where density of fourth instars was below about three per square meter. Above this density, no clear relation appeared between density and survival.

Components of Late Survival

Late Larval-Early Pupal Survival

Late survival is a function of survival from fourth instar to pupae remaining after predation, or residual pupae (late larval-early pupal survival) (fig. 4). Both rates ranged across about 15-fold, and they varied together ($r^2 = 0.85$). Similarly, Morris (1963) found a particularly close correlation in populations of the eastern budworm between survival during fourth through sixth instars and generation survival.

Figure 4.--Survival from fourth instar to residual pupae (late larval-early pupal survival) versus survival from fourth instar to adult females (late survival). Data from populations studied in the Pacific Northwest (1978-82).

4
Figure

Both historically and during the past few years, much research has been devoted to events that occur during the large larval-early pupal interval. For this reason, description and discussion of the principal mortality-causing processes that operate during this interval are presented in a separate section.

Survival of Residual Pupae

Among the populations studied in the Pacific Northwest, survival of the residual pupae ranged from about 25 to 100 percent. Except for two populations in north-central Washington, however, the lowest survival observed was about 50 percent. In general, survival of residual pupae was lower in north-central Washington than in the other areas.

Most of the variability in survival of residual pupae was induced by mortality from parasites (Campbell and others 1983a, Torgersen and others 1983). Among those populations, pupal parasitism ranged from a trace to 51 percent (Torgersen and others 1983). Parasites also appear to be a principal cause of mortality during this interval in other areas. For example, pupal parasitism accounted for 43 percent of pupal mortality among the Colorado populations studied by McKnight (1971).

Variation in the survival of residual pupae played a generally minor role among western populations that have been intensively studied.

Proportion of Females

In 22 of 24 Pacific Northwest populations, the sex ratio among pupae was 1:1. In 21 of these populations, the sex ratio among adults was also 1:1. In all populations, differences between survival of male and female pupae were attributed to chance. The proportion of females among pupae did not differ on Douglas-fir and grand fir, was slightly but significantly higher in the midcrown than in the lower crown, and was significantly higher in the one site studied where average defoliation of current-year shoots was greater than 50 percent (Campbell and others 1983c).

Other investigators have also noted only minor departures from 1:1 in the adult sex ratio in populations of both the eastern and the western budworms. In New Brunswick, Miller (1963a) reported that the proportion of females ranged from 0.33 to 0.54. Miller concluded that "... this proportion did not differ markedly from the expected value of 0.50 during the outbreak, and changes that did occur had a negligible effect on generation survival and population trend." For these same data, Morris (1963) found almost no correlation between the proportion of females and generation survival ($r^2 = 0.01$).

In Colorado, McKnight (1971) found that the proportion of females among adults varied from 0.30 to 0.62. McKnight thought that differential mortality among the subadult male and female insects was probably because

of the more rapid development of the male pupae, which would make them more susceptible to predation by both spruce coneworm larvae and female larvae of their own species.

Variation in the proportion of females among adults appears to have had a negligible effect on populations that have thus far been studied.

LATE LARVAL-EARLY PUPAL SURVIVAL

Density Versus Late Larval-Early Pupal Survival

Late larval-early pupal survival is shown as a function of fourth-instar density in fig. 5. Up to about 30 insects per square meter, these data show an inverse relation between density and late larval-early pupal survival. Above that density, the data are too sparse to discern any underlying relation.

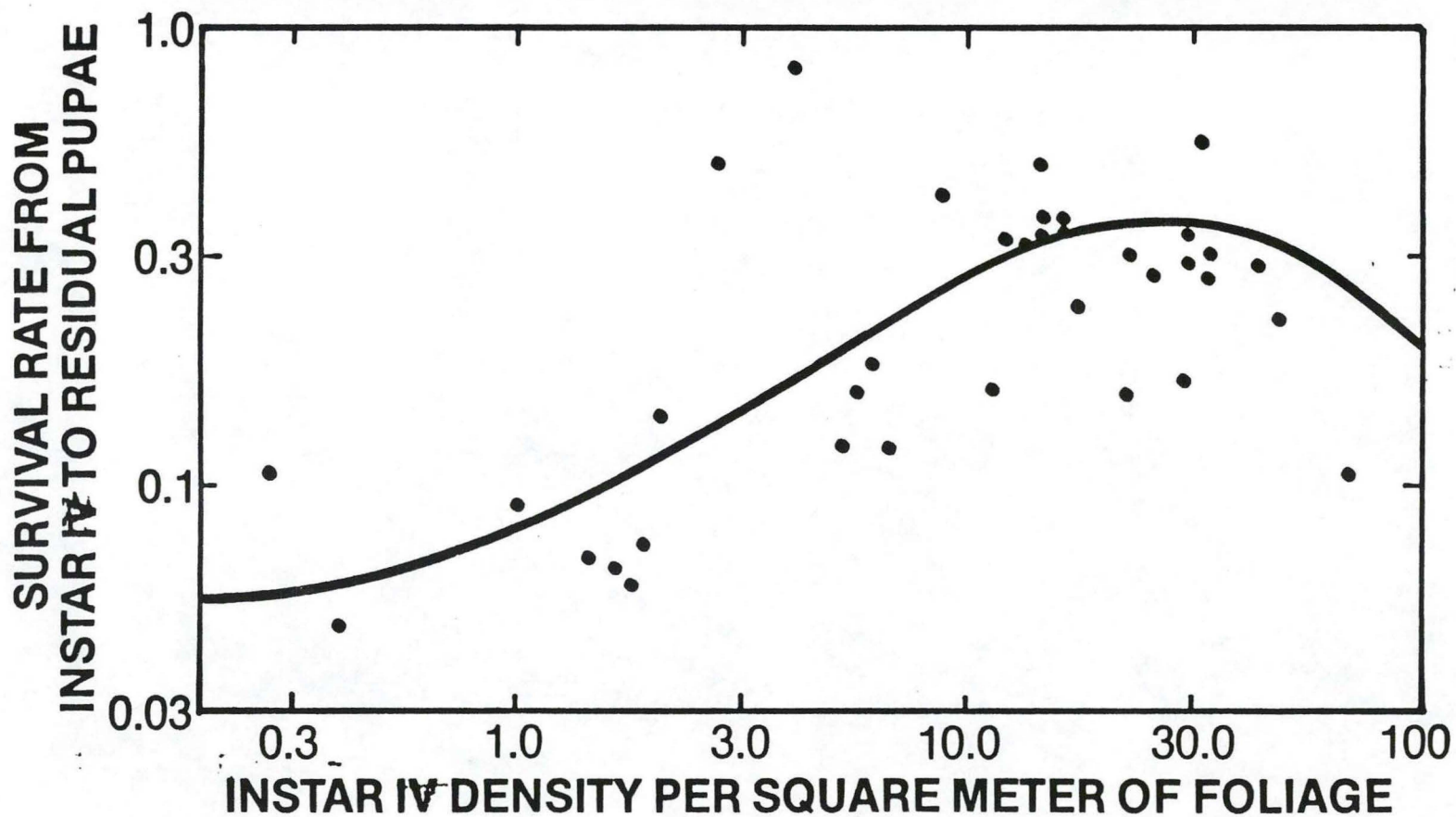
For western budworm, our records stop at about 100 fourth instars per square meter. For eastern budworm, Watt (1963) showed that late larval survival continued to increase slightly to about 140 fourth instars per square meter. Ultimately, as densities increased beyond that point, average survival decreased.

Obviously, fourth-instar density commonly exceeds 80 per square meter among populations of the eastern budworm. Conversely, fourth-instar densities of western budworm greater than about 100 per square meter were not found in either the Pacific Northwest or in northern New Mexico by Stein and McDonnell (1982 unpubl.).

Figure 5.--Fourth-instar density versus subsequent survival from fourth instar to residual pupae (late larval-early pupal survival). Data from populations studied in the Pacific Northwest (1978-82).

figure 5

DENSITY VS. LATE LARVAL-EARLY PUPAL SURVIVAL



As described earlier, the apparent upper limit on fourth-instar densities in the northern New Mexico populations was induced by an inverse relation between egg density and early survival (fig. 3). No similar relation has been suggested for the eastern budworm. If this major apparent difference between the numerical behavior of the two budworm species proves to be general, it should provide much of the basis for understanding both the relatively indeterminate duration of outbreaks by the western species and the relatively mild biological effects of those outbreaks, compared to these same attributes of the life system of the eastern budworm.

Components of Late Larval-Early Pupal Survival

Role of Parasites

The bulk of our information about natural enemies of both the eastern and western budworms has been obtained during outbreaks, and to some extent during the decline phase of these outbreaks. Varty (1974) indicated that about 150 species of arthropods attack the budworms, and that about a third of these are predators.

Eighteen species of parasites were consistently represented in rearings from populations of the budworm studied recently in the Northwest.

Torgersen and others (1983) listed the species as follows, in approximate order of decreasing dominance:

Apanteles fumiferanae Viereck, Glypta fumiferanae (Viereck),
Charmon gracile (Provancher), Enytus montanus (Ashmead), and
Mesochorus tachypus Holmgren--a secondary parasite; all from
larvae. Species reared from pupae were: Agria housei Shewell,
Madremyia saundersii (Williston), Ceromasia auricaudata Townsend,
Phaeogenes maculicornis hariolus (Cresson), Itoplectis
quadricingulata (Provancher), Ephialtes ontario (Cresson),
Phorocera incrassata Smith, and Timavia fumiferanae (Tothill).
Trichogramma minutum (Riley) was the only parasite reared from
budworm eggs.

The percentage contribution of parasitism to total killing power
(equivalent to the killing power of Varley and Gradwell (1960)) was
lowest among the populations in Idaho and Oregon, intermediate in
Montana, and highest in Washington (table 1). Because the contribution
of parasites was highest in Washington where the populations had been
decreasing for several years, parasites may have been playing an active
role in regulating these declining populations (Torgersen and others
1983).

Table 1--Percentage contributions of larval and pupal parasitism to total killing power during the budworm generation, and during the interval from fourth instar to adults (after Torgersen and others 1983).

Location	Number of sites	<u>Average percent contributed to:</u>	
		Generation	Interval
<u>Larval parasitism</u>			
Washington	5	5.7	18.0
Idaho	4	2.7	9.5
Montana	4	4.5	8.2
Oregon	2	3.5	6.5
<u>Pupal parasitism</u>			
Washington	5	13.2	30.2
Idaho	4	1.3	4.5
Montana	4	4.5	9.7
Oregon	2	1.0	2.0

Several investigators have concluded that parasites play a substantial part in regulation of eastern budworm at sparse densities, but that their potential for rapid numerical response can not curtail host numbers once release has begun (Blais 1960, Dowden and others 1948, Graham and Orr 1940, Miller 1963b, Tothill 1923). Morris and others (1958a) believed that the pronounced delayed response of parasites was compounded by adult dispersal behavior of the eastern budworm, which could dilute or destroy developing synchronization between the budworm population and its parasite complex. (This same observation could also apply to other natural enemies.) Apparent increases in parasitization during a decline of the budworm could simply indicate that the residual population, which has already suffered heavy losses, is immediately subject to pressure from a parasite complex that is still increasing in response to the former density of the host.

Role of Birds and Ants

At the start of the CANUSA program, information about the role of birds in the West was limited to a record attributing the collapse of an outbreak at Lillooet, British Columbia, to the joint effects of birds and parasites (Wilkes 1946). In contrast, a wealth of information was available on the role of birds in the dynamics of budworm populations in the East. They had been identified as playing significant roles in terminating outbreaks of the eastern budworm (Blais and Parks 1964, Dowden and others 1950, Jaynes and Drooz 1952). Dowden and others (1948,

1953) found that about 15 species of resident and nonresident birds fed heavily on the eastern budworm. Shooting-out techniques by Dowden and others (1953) and caging studies by Jaynes and Drooz (1952) demonstrated striking quantitative effects of excluding birds (and parasites) from individual trees and entire plots.

Detailed studies on avian predation on the eastern budworm (Mook 1963, Morris and others 1958b) indicate that predation by birds was greatest during the sixth-instar and pupal stages. All bird species, particularly three warblers, showed pronounced, direct numerical responses to budworm density. Graham and Orr (1940) suggested that the scarcity of insectivorous birds brought on by a combination of unfavorable weather and lack of food may have stimulated an eastern budworm outbreak in Minnesota. Most recently, Crawford and others (1983) concluded that birds ate about 2, 23, and 87 percent of the insects in sparse, transition, and dense populations of the eastern budworm.

In 1979, several species of birds were commonly observed preying on the western budworm. These species included evening grosbeak (Hesperiphona vespertina), pine siskin (Spinus pinus), chipping sparrow (Spizella passerina), darkeyed junco (Junco hyemalis), and western tanager (Piranga ludoviciana) (Garton 1980 unpubl.). Two sites, with single-branch bird exclosures (Campbell and others 1981) had pupal densities on protected branches twice as high as on control branches (Torgersen and Campbell 1982).

Ants were also seen investigating and eating the budworm. In 1980, to cite an extreme example, 96 separate observations were made of ants investigating or eating pupae in one site in northcentral Washington (Campbell and Torgersen 1982). Species of ants observed eating budworm pupae between 1979 and 1982 include the following: Camponotus modoc Wheeler, C. vicinus Mayr, C. laevigatus (Smith), Formica haemorrhoidalis Emery, F. accreta Francoeur, F. podzolica Francoeur, F. neorufibarbis Emery, and F. lasiodes Emery (Youngs and Campbell 1982 unpubl.).

Ant predation on both the eastern and western budworms has been observed by other investigators. Mathers (1932) in British Columbia and Thomson (1957) in Ontario considered ants important budworm predators, and both Bain (1974 unpubl.) and Markin (1979 unpubl.) identified ants as predators of the western species.

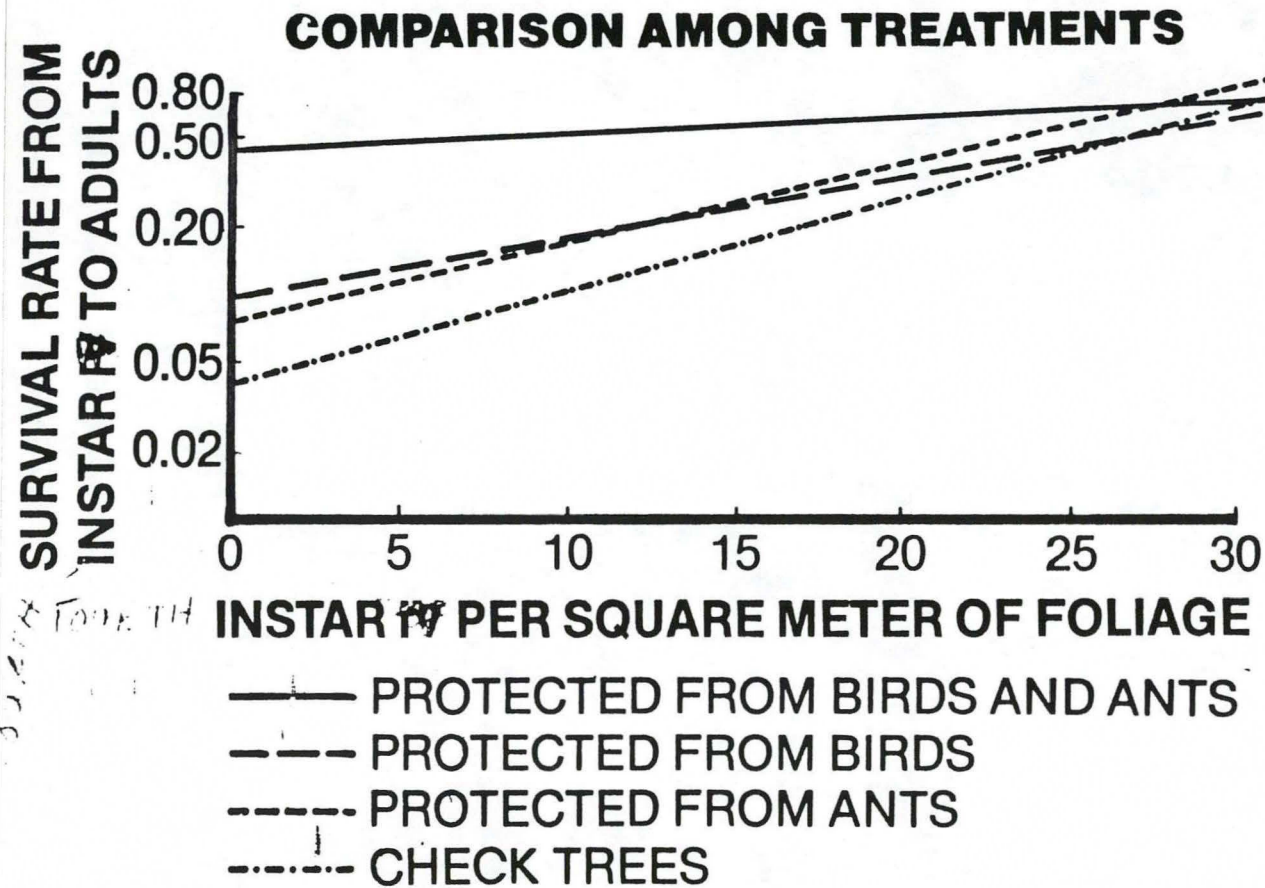
In 1980, whole-tree exclosures and sticky barriers were used to exclude avian predators, predaceous ants, or both from 9-m-tall (29.5-ft), open-grown trees on one site in north-central Washington and four sites in central Idaho. Budworm on these trees were protected from about the fourth instar until they either died or became adults. At the lowest budworm density (1.7 fourth instars per square meter), 10 to 15 times as many adult moths were produced on trees protected from both birds and ants as on control trees. Even when fourth-instar density was 25 insects per square meter, adult density continued to be about twice as high on protected trees as on controls. Birds alone or ants alone were usually sufficient to greatly dampen the high survival observed when both groups were excluded (fig. 6).

Figure 6.--Fourth-instar density versus survival on trees protected from birds, ants, and both groups, and on control trees (after Campbell and others 1983b).

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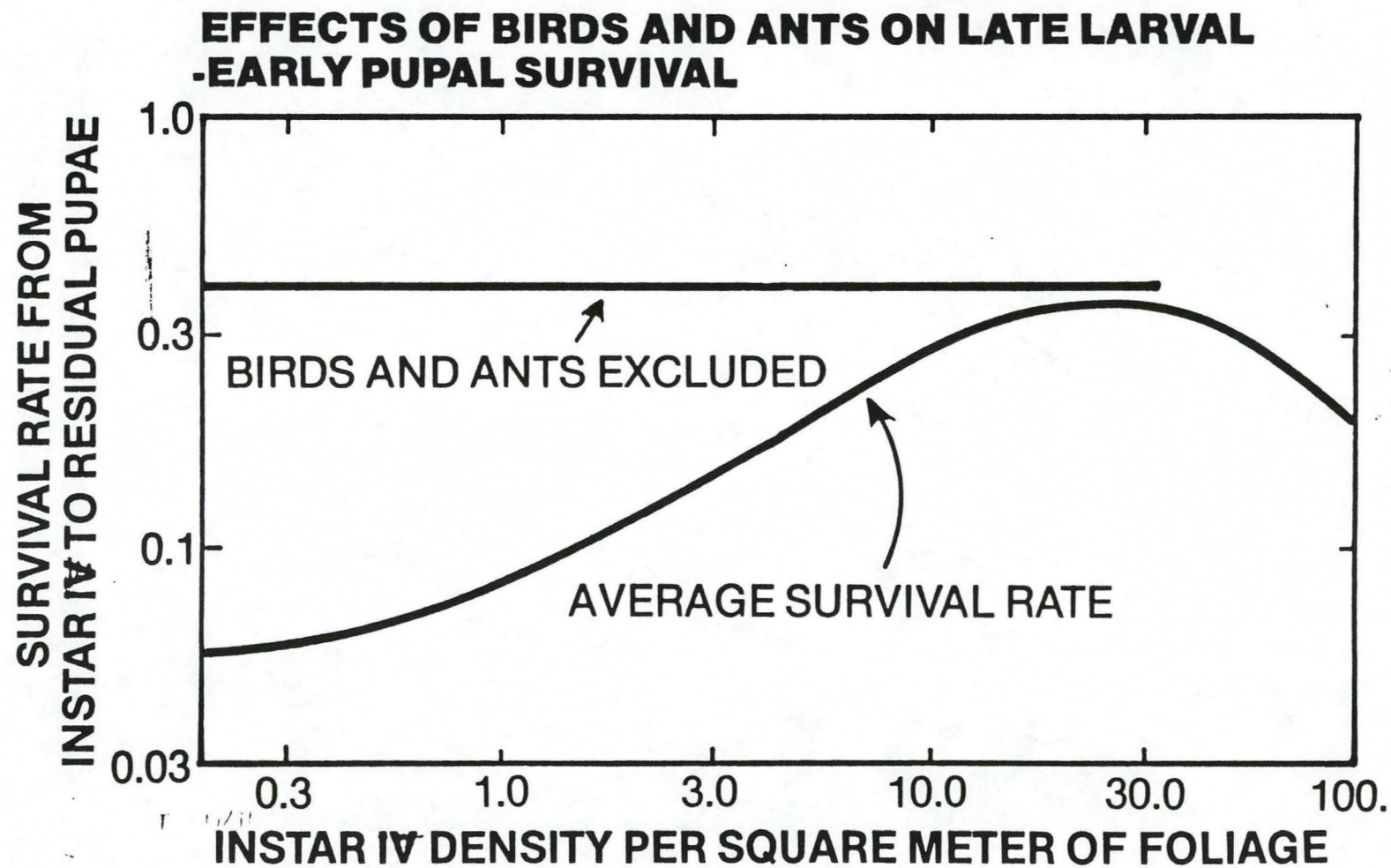
figure 6



In 1981, the trials initiated in 1980 with whole-tree exclosures and sticky barriers were continued on sites in northwest Montana and eastern Oregon. Again, the results showed a strong inverse relation between budworm density and the effects of birds and ants. This predation, combined with mortality from all other sources, was consistently adequate to reduce survival across the late larval-early pupal interval to about 5 percent in populations with fourth-instar density less than one insect per square meter. When these predators were removed, however, average survival increased to about 40 percent (fig. 7). Unless other processes--such as inflight of gravid females--upset low-density stability, predation by birds and ants can maintain most budworm populations in the Pacific Northwest at sparse densities indefinitely.

Figure 7.--Fourth-instar density versus survival from fourth instar to residual pupae, on both trees where birds and ants had been excluded and control trees. Data from populations studied in the Pacific Northwest (1978-82).

figure 7



The relative influence of birds versus ants can be greatly influenced by stand age and structure. For example, birds were as effective in destroying pupae on branches in the upper crowns of tall trees as on branches at about breast height; ants, however, were only effective on low branches (Campbell and Torgersen 1983a). In contrast to the dominance of birds on tall trees, the roles of birds and ants tend to be reversed on seedlings (Campbell and others 1983 unpubl.).

Other Mortality-Causing Factors

Casual observations have shown that insectivorous mammals eat both late instars and pupae. No attempt has been made, however, to quantify the effect of this predation. In the East, Morris (1955) noted that most of the large larvae that drop to the understory are eaten by white-footed mice, Peromyscus leucopus Rafinesque. As an influence on eastern budworm population dynamics, however, small mammals have essentially no effect (Morris and others 1958b).

The activity of arthropod predators is seldom reported. Brief mention is made of predation by representatives of several groups, such as a clerid beetle and a snake fly (Carolin 1974), a carabid beetle (Sanders and Frankenhuyzen 1979), and mites (Jaynes and Drooz 1952). But most of the interest in arthropod predators of the budworms has been in spiders (Loughton and others 1963, Turnbull 1956). These authors concluded that

spiders take whatever prey is most abundant, and that by sheer weight of numbers they are important in budworm regulation. The web-spinning therediids and the hunting salticids constitute the dominant families known to prey on budworm.

Four groups of microorganisms--microsporidia, viruses, bacteria, and fungi--are known to occur in all budworm stages except the egg. The relevant literature was reviewed by Nielson (1963), who concluded that the diseases affecting the eastern budworm are only mildly infectious and have low epidemiological potential. In populations studied in the Pacific Northwest between 1978 and 1982, only a very few specimens showed symptoms of a lethal infectious or noninfectious disease.

At least across the interval from fourth instar to adults, survival of populations in the Northwest consistently approached a high constant on trees that had been protected from birds and ants (fig. 7). Increased mortality from some other sources did not effectively compensate for the absence. In short, other mortality-causing factors played a minor role in regulating late survival, once birds and ants had been excluded (Campbell and Torgersen 1983b).

Foliage Quality

Recently, several investigators have examined relations between the natural defensive chemistry of Douglas-fir and success of the western budworm. To explore some of the reasons why populations rarely reach outbreak densities west of the Cascade Range, Perry and Pitman (1983) tested responses of larvae to foliage from seedlings of both west-side Douglas-fir (var. menziesii) and interior Douglas-fir (var. glauca) grown in the same west-side garden. Surprisingly, foliage from the interior Douglas-fir caused a wide range of larval mortality; foliage from the west-side Douglas-fir caused no significant larval mortality. Perry and Pitman concluded that environmental factors in continental environments may alter the ability of the trees to produce allelochemicals, and thus play a key role in regulating interior populations. They concluded that the apparent lack of defensive chemicals in west-side Douglas-fir suggests either that "inducible defenses may play a role" or that predators and parasites may keep budworm populations at low densities in west-side ecosystems.

Studies by Cates and others (1983a, 1983b) indicate that the terpene complement associated with resistant trees in Montana was different from that found in New Mexico. From agar-diet studies, they found that high concentrations of bornyl acetate and beta-pinene--similar to the concentrations found in the foliage of resistant trees--increased the

duration of the larval stage and decreased dry-weight production of the larvae. Available foliar nitrogen did not appear to be important, but trees that flushed relatively late in the season harbored fewer larvae and sustained less defoliation.

OBSERVED EGGS PER FEMALE

In the Pacific Northwest, the number of eggs deposited for each female pupal case that was produced (observed eggs per female), ranged across about 100-fold, from a low of about 10 to a high of about 1,000. The correlation between observed eggs per female and annual trend is $r^2 = 0.25$. As suggested earlier (Campbell and others 1983a), both the range in the number of eggs deposited per female and the correlation between this number and annual trend show that variation in observed eggs per female has an important influence on the dynamics of this life system.

Although many complex processes are involved (Greenbank and others 1980), observed eggs per female moth is the result of both the average fecundity of those moths at the time they emerge, and the net result of all the processes of migration and mortality that influence those moths until they die or finish laying their eggs.

Fecundity

In any population, average fecundity can be estimated by rearing a sample of mated female moths and counting the eggs they produce. Fecundity is affected largely by the quantity and quality of food available to the preceding larvae (Blais 1952, Miller 1963c). Other extrinsic factors that may affect fecundity indirectly include weather (Greenbank 1956), the availability of suitable places to lay eggs, and disease (Neilson

1963). In populations of both the eastern and the western budworms, mean fecundity is closely correlated with the size or weight of the female pupae (Kirkbride and Wagner 1983 unpubl., Miller 1957).

Average fecundities ranged from about 100 to 200 among the populations studied in the Pacific Northwest. Almost no correlation was found between these fecundities and the observed number of eggs per female ($r^2 = 0.03$). Apparently, variation in average fecundity had almost no effect on the number of eggs actually deposited per female moth.

Index of Adult Dispersal

The net results of moth migration and mortality (index of adult dispersal) can be estimated from the ratio between egg density on the foliage and the innate egg-laying ability of the emerging females. Relation of the index of adult dispersal to observed eggs per female (fig. 8) are very close ($r^2 = 0.92$). Thus, almost all of the variation in observed eggs per female resulted from variation in adult migration and mortality. Immigration clearly exceeded the combined effects of emigration and mortality where observed eggs per female were greater than the inherent ability of females to produce eggs (about 200). Significantly, observed eggs per female were consistently much greater than 200 among the populations we studied in eastern Oregon at the start of the current outbreak. Just as in eastern budworm, redistribution of adult female moths is a major factor in the population dynamics of the western species.

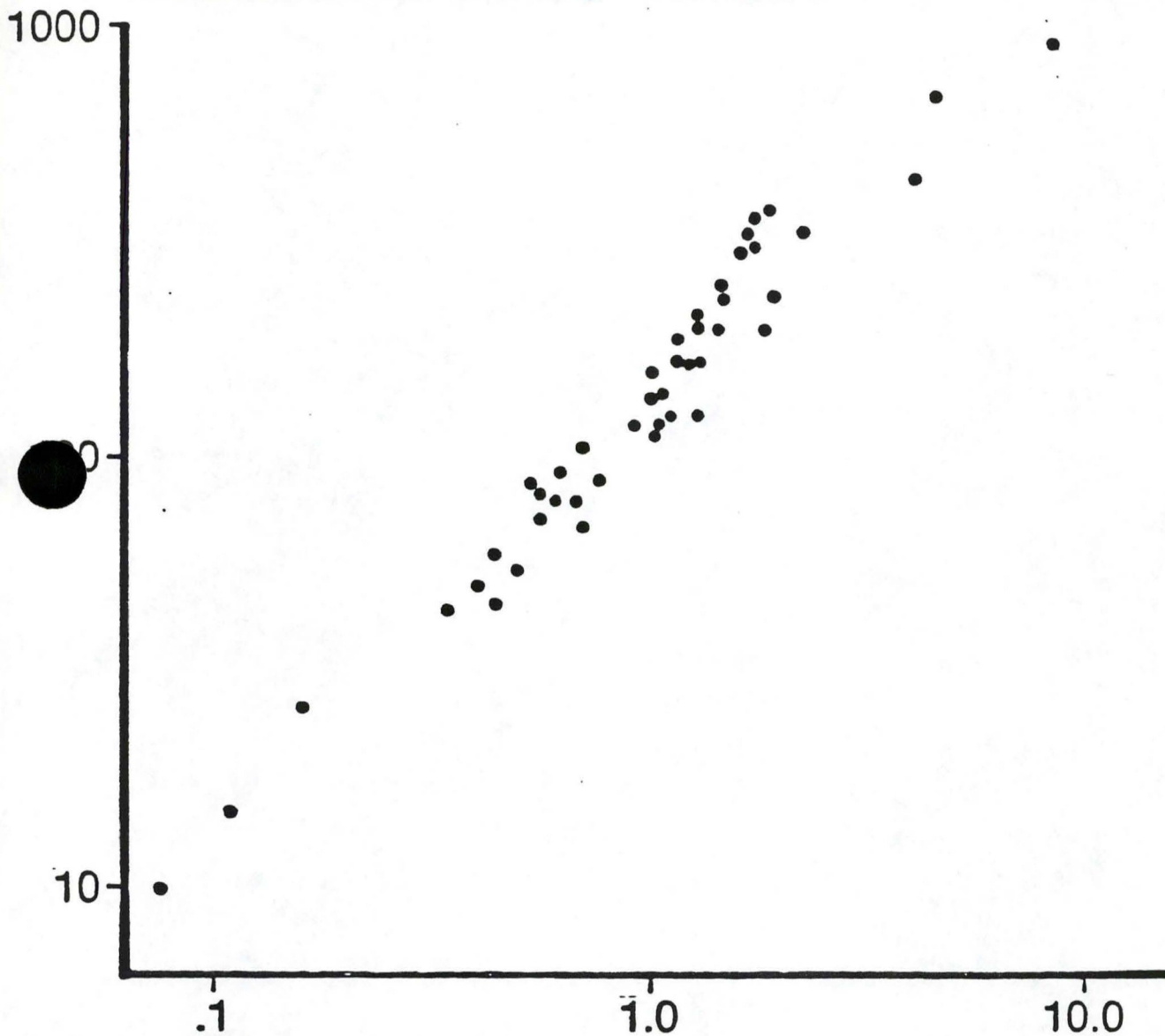
Figure 8.--Adult dispersal index versus observed eggs per female. Data from populations studied in the Pacific Northwest (1978-82).

8

Figure

of

~~ADULT DISPERSAL INDEX VS.~~
~~OBSERVED EGGS PER FEMALE~~



~~RATIO BETWEEN OBSERVED~~
~~AND EXPECTED EGG DENSITY~~
INDEX OF ADULT DISPERSAL

Density of Adult Females Versus Egg Density

By the spring of 1981, redistribution of adult females clearly seemed to be a major factor in western budworm population dynamics (Campbell and others 1983b). Consequently, the life-table studies were supplemented with data from ten additional sites; six in southwestern Montana and four in eastern Oregon. Both adult female densities and subsequent egg densities per square meter were estimated on each of these additional sites.

Egg density in the 46 Northwest populations was examined as a function of both the density of preceding adult females and an index of defoliation. This index, based on average defoliation of current-year shoots, was:

No defoliation = 1;

$0 < \text{defoliation} \leq 25 \text{ percent} = 2$;

$25 \text{ percent} < \text{defoliation} \leq 50 \text{ percent} = 3$; and

$50 \text{ percent} < \text{defoliation} \leq 75 \text{ percent} = 4$.

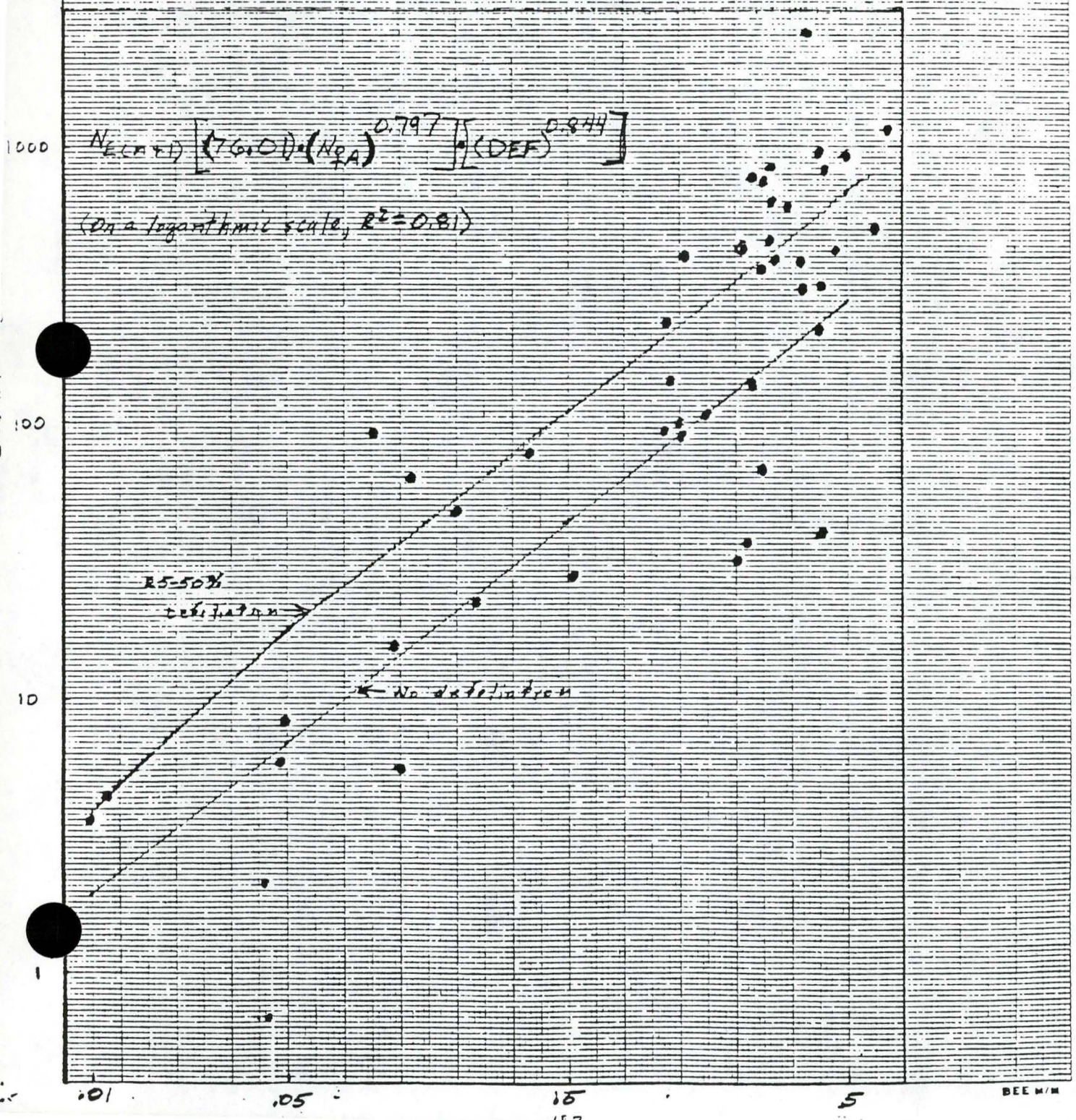
(Average defoliation of current-year shoots never exceeded 75 percent among the populations studied.)

Relations between adult female moths, defoliation, and subsequent egg density are shown in figure 9. Only 15 of the 46 predicted values (33 percent) were within ± 20 percent of their observed values. Seventeen predicted values (36 percent) deviated from observed by more than ± 75 percent.

Figure 9.--Density of emerging adult females (N_{OA}) and an index of defoliation (DEF), versus subsequent egg density ($N_{E(n+1)}$). Data from populations studied in the Pacific Northwest (1978-82).

Figure 9

Density of Adult Females versus Egg Density



Perhaps much of the variation in the density of eggs not associated with either the density of adult females or defoliation will prove to be a function of identifiable characteristics of sites and stands. Only further studies can provide an answer..

CONCLUSIONS AND RECOMMENDATIONS

In the absence of factors that upset low-density stability, most sparse populations of western budworm can remain at sparse densities indefinitely. Most of this low-density stability is induced by predaceous birds and ants. Outbreaks can be initiated when eggs are redistributed and aggregated by the adult moths, when early survival is exceptionally high, or when both of these events occur more or less simultaneously.

Outbreaks persist, in part, because density-dependent mortality among small larvae thins the population, thus reducing the chance of subsequent foliage exhaustion and subsequent mass starvation.

Outbreak collapse can occur through many processes, or combinations of processes. Currently, such collapses can only be predicted probabilistically.

WORK REMAINING ON STUDY

Almost invariably, research on the dynamics of forest pests has concentrated on outbreaks. In contrast, recent studies on the dynamics of the western budworm have concentrated on the processes that maintain or release sparse populations. Consequently, we know most about the dynamics of western budworm populations when these populations are sparse. In addition to further work on sparse populations, follow-up studies should be designed to understand the outbreak dynamics of the western budworm.

COOPERATION AND COORDINATION

Cooperation and coordination with other investigators has been satisfactory.

PROBLEMS ENCOUNTERED

No noteworthy problems were encountered.

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